

Contrasting Modes of Reproduction in Two Antarctic Asteroids of the Genus *Porania*, With a Description of Unusual Feeding and Non-feeding Larval Types

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Abstract. Reproduction and development were markedly different in two morphologically similar asteroids of the genus *Porania* that occur in shallow waters of McMurdo Sound, Antarctica. Adults of the recognized species, *Porania antarctica* (Perrier, 1894), are large ($R_{\max} = 70$ mm) and have genital pores that are situated aborally on the disc; females broadcast spawn large numbers ($3\text{--}4 \times 10^3$) of buoyant eggs that measure 0.55 mm and develop into unusual, yolky planktotrophic larvae. In contrast, adults of the undescribed *Porania* sp. are considerably smaller ($R_{\max} = 30$ mm) and their genital pores are located orally on the disc. Female fecundity is low (100–310 eggs); the few eggs produced measure 0.55 mm, are heavier than seawater, and develop into demersal lecithotrophic larvae. These differences conform to general patterns reported for echinoderms with divergent types of reproduction. However, other differences contradict established trends; specifically, *P. antarctica* with planktotrophic development has a shorter embryonic and larval phase (65 days vs. 78 days) and a larger juvenile size at metamorphosis (0.8 vs. 0.6 mm) than *Porania* sp., which has lecithotrophic development. The reproduction of *P. antarctica* incorporates advantages of both planktotrophic and lecithotrophic strategies and may be particularly well-suited for environmental conditions in the Antarctic Ocean.

Introduction

The larval development of echinoderms can be classified into general categories on the basis of mode of nutrition and habitat (Chia, 1974). Larvae may be lecitho-

trophic (non-feeding) or planktotrophic (feeding on particulate material); lecithotrophic larvae can be pelagic, demersal, or brooded, whereas planktotrophic larvae are nearly always pelagic (Young and Chia, 1987). Species with lecithotrophic development typically have a larger maximum egg size, reduced fecundity, abbreviated larval development, and greater juvenile size at metamorphosis than species with planktotrophic development (Strathmann, 1985; Emlet *et al.*, 1987). Intermediate reproductive strategies (*e.g.*, facultative planktotrophy), considered transitional and evolutionarily unstable by some theoretical modelers (Vance, 1973; Christiansen and Fenchel, 1979), are known or implied for several species of echinoids (Strathmann, 1979; Emlet, 1986) but seem to be generally rare among echinoderms.

Phylogenetically proximate echinoderm species that are nearly indistinguishable by morphological criteria often occur sympatrically and exhibit contrasting developmental strategies. With such strong similarities between species, these complexes provide useful systems for reliable analyses of the interrelationship between different reproductive traits (*e.g.*, egg size, larval type, juvenile size) and as such they have been the focus of several investigations (Atwood, 1973; Menge, 1975; Lawson-Kerr and Anderson, 1978; Emson and Crump, 1979; Scheibling and Lawrence, 1982; Emlet, 1986).

A pair of morphologically similar asteroids of the genus *Porania* co-occur in shallow waters of McMurdo Sound, Antarctica. The two types can be distinguished reliably by the position of the genital pores, which are found on the aboral surface in the recognized species, *Porania antarctica* (Perrier, 1894), and on the oral surface in the undescribed form, referred to here as *Porania* sp. This contrast was first recognized by H. E. S. Clark

(1963) and A. M. Clark (1962), who argued that a higher taxonomic ranking was warranted for the undescribed form. However, their observations did not lead to the description of a new species and at present the taxonomic standing of *Porania* sp. is unresolved (H. E. S. Clark, pers. comm.).

This paper describes differences in reproduction and development between *Porania antarctica* and *Porania* sp. that substantiate Clark's (1962) recommendation of distinct species rankings for the two forms. The findings of this study are compared to general patterns of reproduction in other echinoderms and discussed in the context of life-history evolution.

Materials and Methods

Adult sea stars were collected haphazardly by SCUBA divers at depths of 10–33 m beneath the annual sea ice in McMurdo Sound between Sept. 1984 and Dec. 1985. Immediately after collection, individuals were transported to McMurdo Station in ice chests filled with ambient seawater and maintained for up to several months in laboratory sea tables with flow-through seawater (-1.5°C). Spawning was induced by injection of 1-methyladenine (1-MA at $1 \times 10^{-4} M$ in seawater) into the coelom. For each species, the diameters of 30–35 eggs selected haphazardly from two spawning females were measured using a compound microscope equipped with an ocular micrometer. The annual fecundity of females was estimated by direct count of spawned eggs for *Porania* sp. and by counting a known portion of the total spawn for *P. antarctica*. Spawned females were maintained in the laboratory for at least one week after a spawning event and treated daily with 1-MA to assure that most mature oocytes had been shed.

Embryos and larvae were reared at temperatures near their ambient (-1.5 to -1.0°C) in gently stirred or unstirred 4 L culture vessels following procedures established by Strathmann (1971), as modified for Antarctic asteroid larvae by Pearse and Bosch (1986). Larvae of *Porania antarctica* were fed every two days with equal amounts of xenic *Isochrysis galbana* and *Dunaliella tertiolecta* to a final concentration of $5\text{--}10 \times 10^3$ cells/ml in $5 \mu\text{m}$ -filtered seawater. No cultured food was added to vessels containing lecithotrophic larvae of *Porania* sp. Brachiolariae with well-developed rudiments were isolated in small glass dishes and induced to settle with substrates (e.g., shell debris, small rocks, sediment) collected from adult habitats. Since competent brachiolariae of *P. antarctica* were usually buoyant, glass slides covered with a bacterial-algal film were suspended horizontally in midwater to facilitate settlement.

Results

Distribution and spawning

Porania antarctica were collected primarily at New Harbor (Fig. 1) during the austral spring and summer,

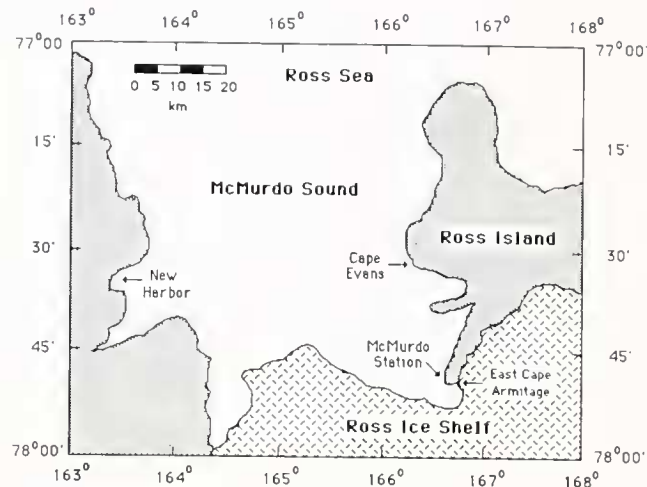


Figure 1. Sites in McMurdo Sound, Antarctica, where *Porania antarctica* and *Porania* sp. were collected.

1984 and 1985, when weather and sea ice conditions permitted access to this remote site. Only a few specimens were collected at E. Cape Armitage and McMurdo Station, usually below depths of 30 m. Adults were large, measuring up to 70 mm from the tip of the longest ray to the center of the disc (R). The ovaries of all females ($n = 11$) examined during the austral spring, 1984 and 1985, were small and contained only a few oocytes of the largest size class. Individuals ($n = 9$) collected in early February, 1985 did not respond to 1-MA; the dissected ovaries of one female were relatively small and devoid of fully grown oocytes. The remaining eight sea stars were maintained in laboratory sea tables until mid October and treated with 1-MA about every two months. Two of four females spawned in late September and the other two in early October. Males contained active sperm from early August to mid-October, as revealed by partial spawnings and biopsies of testicular lobes. Gametes were broadcast through aboral genital pores. Spawned oocytes, approximately $3\text{--}4 \times 10^4$ in number ($n = 2$ females), were of moderate size ($548 \pm 10 \mu\text{m}$, $n = 30$), opaque yellow in color, and buoyant.

Individuals of *Porania* sp. were generally rare and only 20 were collected during this study: 14 from East Cape Armitage, and 3, 2, and 1 from McMurdo Station, Cape Evans, and New Harbor, respectively. Adults were small, with R ranging from 10–30 mm. Females were induced to spawn with 1-MA in November ($n = 2$) and December ($n = 1$), 1984, and in February ($n = 1$), April ($n = 2$), and July ($n = 1$), 1985. Males examined during each of these sampling dates contained active sperm. Although similar in size ($554 \pm 16 \mu\text{m}$, $n = 35$) and lipid content (50–60% of dry weight; J. McClintock, unpubl. data) to the eggs of *Porania antarctica*, the few eggs (100–310, $n = 4$) produced by *Porania* sp. were free-spawned through oral

Table I

Embryonic and planktotrophic larval development of Porania antarctica reared at -1.5 to -1.0°C

Developmental stage	First appearance (days)	Size* (mm)
Zygote	0	0.55
Two-cell embryo	0.42	—
Coeloblastula	3.2	—
Hatched blastula	5.8	—
Gastrula	12	0.70
Bi-lobed larva	20	0.76
Bipinnaria	22	0.80
Brachiolaria	40	1.1
Juvenile	65	0.79

* Refer to the diameter of zygotes and juveniles and the maximum length of all other stages.

genital pores and immediately settled onto the bottom of culture dishes.

Planktotrophic development of Porania antarctica

With several important exceptions described below, the development from fertilization to metamorphosis of *Porania antarctica* is similar to that of the north temperate asteroid *Porania pulvillus* (Gemmill, 1915) and generally follows the typical pattern of asteroids with feeding larvae (Table I).

Early cleavage divisions were slow at -1.5 to -1.0°C ; morula and blastula stages were reached approximately 2.0 and 3.2 days after fertilization, respectively. By the fifth day of development, blastulae had developed a rich, active ciliary field. Hatched blastulae were highly buoyant and seemed to have little control over their vertical position; they usually floated near the water surface in stirred as well as unstirred culture vessels. Gastrulation by invagination was accompanied by substantial expansion of the larva, which attained a length of nearly 0.7 mm by the 12th day of development.

Young bipinnariae were large, and judging from their coloration and buoyancy, retained a substantial proportion of the maternal yolk. At this stage the mouth is open and connects to the digestive tract, which is divided into an esophagus, stomach, and intestine. There followed a period of significant differentiation but of little apparent increase in size, as evidenced by the extension of the axo-hydrocoels, which by the 27th day had fused anteriorly forming a U-shape around the esophagus.

After 32 days of development, an adhesive disc formed in the presumptive region of the brachiolarian complex. Brachiolarian arms were first observed on the 40th day of development. The various ciliated arms characteristic of planktotrophic asteroid larvae are lacking in *Porania antarctica*. Early brachiolariae measured 1.1 mm in

length and grew very little to attain their final form (Fig. 2). Over the next 25 days, the brachiolarian arms increased gradually in size and developed an arrangement of adhesive papillae. Sixty-five days after fertilization, the larvae were competent to metamorphose. Some would swim along the bottom of dishes and temporarily attach themselves by their brachiolarian arms. However, most fully developed brachiolariae (83%, $n = 53$) were positively buoyant and remained near the water surface. They attached and metamorphosed on the sides of dishes and underneath floating objects rather than on the bottom. Newly metamorphosed juveniles ($0.79 \pm .04$ mm diameter, $n = 9$) had well-differentiated arms and retained the opaque, yellowish coloration of the egg.

Lecithotrophic development of Porania sp.

A chronology of development is given in Table II. Early cleavage followed the typical pattern of asteroids, but the rate of development was extremely slow; an early blastula stage was not reached until 12 days after fertilization. Embryos hatched as ciliated blastulae that were negatively buoyant and moved along the bottom of culture vessels by ciliary action. Gastrulation was by invagination, leading to the formation of a blastopore that was widely open at first, but gradually narrowed and disappeared during later stages of development. The gastrula reached 0.6 mm by the 26th day of development, when a small lobe first became evident on the anterior end (Fig. 3A). Continued expansion in this fashion resulted in the formation of a generally ciliated, pear-shaped larva that consisted of a large, rounded posterior lobe and a narrow

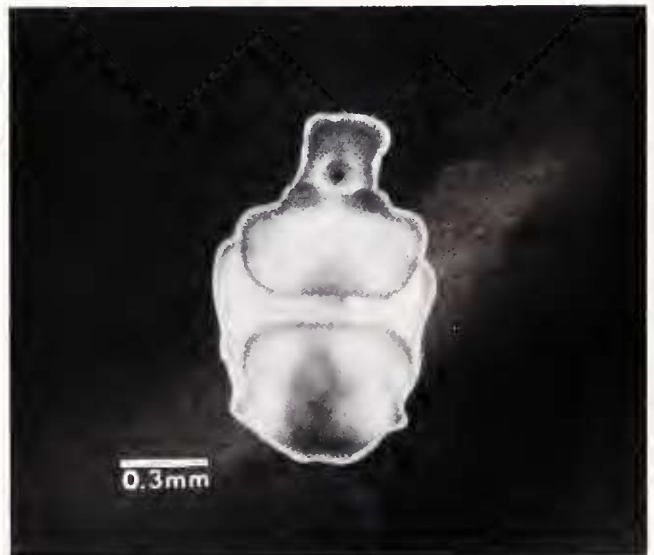


Figure 2. Feeding brachiolaria of *Porania antarctica*. The opacity of this larva is likely due to an abundance of yolk. Note the absence of ciliated larval arms, which are typically used in swimming and feeding by planktotrophic asteroid larvae.

Table II

Embryonic and lecithotrophic larval development of the undescribed asteroid Porania sp. reared at -1.5 to -1.0°C

Developmental stage	First appearance (days)	Size* (mm)
Zygote	0	0.55
Hatched blastula	15	—
Early gastrula	21	0.57
Late gastrula	26	0.60
Pear-shaped larva	38	0.76
Early brachiolaria	47	0.80
Late brachiolaria	68	1.20
Juvenile	75	0.60

* Refer to the diameter of zygotes and juveniles and the maximum length of all other stages.

anterior lobe and was entirely lacking feeding structures (Fig. 3B). These larvae were negatively buoyant and usually swam near or on the bottom of stirred and unstirred culture vessels with the anterior lobe foremost and the anterioposterior axis in a horizontal attitude.

Three bulbous arms first formed 47 days after fertilization: a single median anterodorsal arm, and a pair of ventrolateral arms that occupy a region near the base of the narrow anterior lobe (Fig. 3C). Soon after, each arm was able to adhere temporarily to glass surfaces, and an adhesive disc had differentiated central to them. Therefore, the larva can be considered a modified brachiolaria. Fully developed brachiolariae (Fig. 3D) measured 1.2 mm in length. Attachment to a substratum was initially accomplished by the brachiolarian arms and the adhesive disc. Metamorphosis included the complete degeneration of the anterior lobe, and lasted from one to two weeks. During this period, some larvae detached from the bottom and continued to swim for hours to days. Final attachment was facilitated by the tube feet of the juvenile rudiment. The newly metamorphosed sea star, about 0.60 ± 0.03 mm across ($n = 10$), had two pairs of tube feet on each of its 5 arms. The arms were short and difficult to distinguish due to the presence of yolk on the aboral surface of the disc.

Discussion

In echinoderms, and particularly asteroids, there are considerable differences (*e.g.*, egg size, larval morphology) between planktotrophic and lecithotrophic developmental strategies (Strathmann, 1974; Emler *et al.*, 1987). One interpretation of this phenomenon is that types of development intermediate of planktotrophy and lecithotrophy are evolutionarily transitional and short lived (Vance, 1973). However, possible intermediate strategies do appear in some species, particularly among echinoids. Planktotrophic echinoplutei of *Clypeaster ro-*

seaceus develop from relatively large eggs and do not require particulate food to complete development to metamorphosis (Emler, 1986). A similar mode of development (*i.e.*, facultative planktotrophy) is suggested for echinoplutei of the spatangoid *Brisaster latifrons* (Strathmann, 1979) and judging from some egg sizes reported by Emler *et al.* (1987) may occur in several other echinoids (*e.g.*, *Sterechinus agassizi*, *Brisaster fragilis*).

Additional studies are necessary to adequately evaluate the ecological and evolutionary significance of the unusual development described here for *Porania antarctica*. Nonetheless, it is evident that features of both lecithotrophic and planktotrophic strategies are manifested in this species. The larvae feed on bacteria (Rivkin *et al.*,

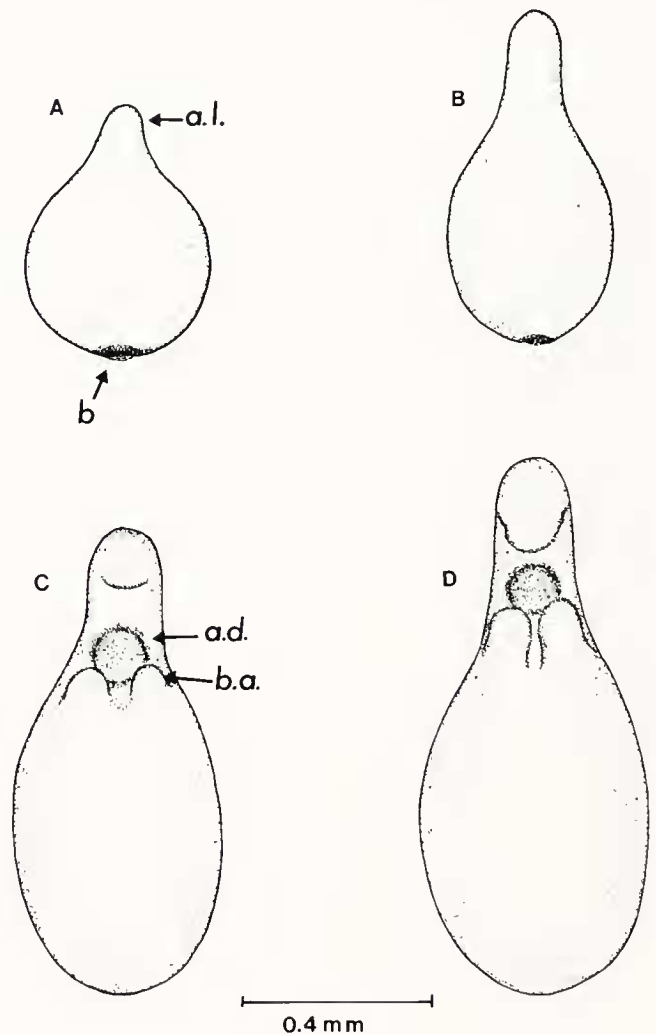


Figure 3. Larval stages of *Porania* sp. (A) Post-gastrula 26 days after fertilization with a small anterior lobe, large posterior lobe, and blastopore. (B) Pear-shaped larva (38 days) showing increased development of the anterior lobe. (C) Early modified brachiolaria 47 days after spawning. Three brachiolarian arms and an adhesive disc have formed on the preoral lobe. (D) Fully developed brachiolaria 68 days after spawning. ad, adhesive disc; al, anterior lobe; b, blastopore; ba, brachiolarian arms.

1986) but, unlike other planktotrophic asteroid larvae, they develop from buoyant eggs containing large lipid yolk reserves (J. McClintock, unpubl. data) and produce an unusually large juvenile at metamorphosis. The characters cited above may contribute to several other unique developmental features of *P. antarctica*. These include: (1) an absence of ciliated arms that aid swimming and feeding in other larvae (Strathmann, 1974), and (2) the metamorphosis of larvae almost exclusively on the sides of culture dishes and undersides of suspended glass slides.

One possible advantage conferred on feeding larvae that develop from larger eggs is an abbreviated larval phase (Vance, 1973; McEdward, 1984; Emlet, 1986). Accordingly, the period from fertilization to metamorphosis of *P. antarctica* is less than half that of another planktotrophic antarctic asteroid, *Odontaster validus* (Pearse and Bosch, 1986). Indeed, at 65 days the developmental period of *P. antarctica* is similar to that of some temperate asteroids reared at their ambient temperatures (Emlet *et al.*, 1987). The production of a fully developed feeding larva from a larger, yolk-laden egg apparently requires less growth and differentiation. In low temperature environments such as the Antarctic, these differences are translated into a considerable reduction in development time, presumably leading to a concomitant decrease in the risk of mortality associated with a pelagic feeding larval phase.

In contrast to *Porania antarctica*, eggs spawned by *Porania sp.* were negatively buoyant. The larvae were lecithotrophic, and judging from their distribution and swimming behavior in culture vessels most likely are demersal in nature. As in *Porania sp.*, larvae of *Asterina minor* also are heavier than seawater and pass through a pear-shaped brachiolaria stage (Komatsu *et al.*, 1979). Hatching of *A. minor* brachiolariae from an attached egg case occurs on the 9th day of development and is followed by a brief (*ca.* 1 day) demersal stage that precedes metamorphosis. In *Porania sp.*, the free-swimming demersal larval phase lasts about two months. With the exception of one other Antarctic sea star, *Acodontaster hodgsoni* (Bosch and Pearse, in press), this is the longest period of development to first metamorphosis reported for asteroids with lecithotrophic larvae (Emlet *et al.*, 1987).

In previous studies of morphologically similar, sympatric asteroids with contrasting developmental strategies (Atwood, 1973; Lawson-Kerr and Anderson, 1978; Emson and Crump, 1979; Scheibling and Lawrence, 1982), distinction of the morphs or species has been made principally on the basis of egg size and embryonic or larval habitat (*e.g.*, pelagic *vs.* brooded). By comparison, the differences reported here for *Porania sp.* and *P. antarctica* (Table III), including sharp contrasts in larval form and mode of nutrition, represent a case of extensive

Table III

Summary of major known differences between *Porania antarctica* and *Porania sp.*

Trait	<i>Porania antarctica</i>	<i>Porania sp.</i>
1) Morphology	Aboral genital pores	Oral genital pores
2) Adult size (R)	Maximum 70 mm	Maximum 30 mm
3) Timing of reproduction	Seasonal (Sept.?–Oct.)	Year-round
4) Fecundity (# eggs)	<i>ca.</i> 35,000	100–310
5) Larval type	Modified planktotrophic, pelagic	Lecithotrophic, demersal

divergence. Such cases are relatively common in some invertebrate taxa, particularly polychaete annelids and gastropod molluscs (Perron, 1981; Hoagland and Robertson, 1988), but seem to be unusual in the Echinodermata.

Among related, sympatric echinoderms, those with larger adults tend to have an extended planktonic larval phase and produce relatively small juveniles at metamorphosis. Small adult size is associated with brooding or an abbreviated non-feeding larval phase and the production of fewer, larger offspring which presumably have a greater chance of survival (*e.g.*, Schoener, 1972; Menge, 1975; Lawson-Kerr and Anderson, 1978; Hendler, 1979). Strathmann and Strathmann (1982) reviewed several possible explanations for this phenomenon. One common explanation links brooding and other forms of non-pelagic development to energetic constraints on reproductive output (Menge, 1975). According to this hypothesis, small adults cannot produce sufficient offspring to benefit from the enhanced dispersal of a typically high-risk pelagic larval phase. In the *Porania* studied here, pelagic feeding development was associated with large adult size and high fecundity in *P. antarctica*. The smaller *Porania sp.* have considerably lower fecundity (*ca.* two orders of magnitude less) and develop non-pelagically. On the other hand, planktotrophic larvae of *P. antarctica* had a shorter developmental period and produced larger juveniles. Therefore, Menge's (1975) hypothesis is applicable only if larval mortality rates in the plankton are much higher than near the bottom. Comparisons of this type have not been made (see Strathmann, 1985; Young and Chia, 1987). One possible consideration is the tendency for pelagic larvae to be swept by currents far from areas suitable for settlement and post-settlement survival, as shown, for example, for continental slope ophiuroids by Gage and Tyler (1981). A second possibility is that predation is much lower on demersal larvae. However, possible larval predators such as polychaetes and small crustaceans are common in shallow antarctic benthic habitats (Oliver, 1979; Marinovic,

1987). Indeed, several species, including the tanaid *Nototanaïs dimorphus* and the small infaunal actinian *Edwardsia meridionalis* often attain mean densities of more than 15,000 m⁻² (Oliver, 1979). How a few larvae produced by *Porania* sp. escape these predators over several weeks of development and recruit successfully into benthic populations is a question of considerable interest.

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Literature Cited

- Atwood, D. G. 1973. Larval development of the asteroid *Echinaster echinophorous*. *Biol. Bull.* **144**: 1–11.
- Bosch, I., and J. S. Pearse. 1989. Developmental types of shallow-water asteroids in McMurdo Sound, Antarctica. *Mar. Biol.*, in press.
- Chia, F.-S. 1974. Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugosl.* **10**: 121–130.
- Christiansen, F. B., and T. M. Fenchel. 1979. Evolution of marine invertebrate reproductive patterns. *Theor. Popul. Biol.* **16**: 267–284.
- Clark, A. M. 1962. Asteroidea. *British Museum Antarctic Exped. Rpts.* Series B, 9: 1–143.
- Clark, H. E. S. 1963. The fauna of the Ross Sea. Part 3. Asteroidea. *N. Z. Dept. Sci. Ind. Res. Bull.* **151**: 1–84.
- Emlet, R., 1986. Facultative planktotrophy in the tropical echinoid *Clypeaster roseaceus* and a comparison with obligate planktotrophy in *Clypeaster subdepressus* (Clypeasteroidea: Echinoidea). *J. Exp. Mar. Biol. Ecol.* **95**: 183–202.
- Emlet, R., L. R. McEdward, and R. R. Strathmann. 1987. Echinoderm larval ecology viewed from the egg. Pp. 145–156 in *Echinoderm Studies 2*, M. Jangoux and J. M. Lawrence, eds. Balkema Press, Holland.
- Emson, R. H., and R. G. Crump. 1979. Description of a new species of *Asterina* (Asteroidea), with an account of its ecology. *J. Mar. Biol. Assoc. U. K.* **59**: 77–94.
- Gage, J. D., and P. A. Tyler. 1981. Non-viable seasonal settlement of larvae of the upper bathyal brittle star *Ophiocten gracilis* in the Rockall Trough abyssal. *Mar. Biol.* **64**: 153–161.
- Gemmill, J. 1915. The larva of the starfish *Porania pulvillus*. *Q. J. Microsc. Sci.* **61**: 27–53.
- Hendler, G. 1979. Sex-reversal and viviparity in *Ophioplepis keiri*, n. sp., with notes on viviparous brittlestars from the Caribbean (Echinodermata: Ophiuroidea). *Proc. Biol. Soc. Wash.* **92**: 783–795.
- Hoagland, K. E., and R. Robertson. 1988. An assessment of poecilogony in marine invertebrates: phenomenon or fantasy? *Biol. Bull.* **174**: 109–125.
- Komatsu, M., Y. T. Kano, H. Yoshizawa, S. Akabane, and C. Oguro. 1979. Reproduction and development of the hermaphroditic sea star, *Asterina minor* Hayashi. *Biol. Bull.* **157**: 258–274.
- Lawson-Kerr, C., and D. T. Anderson. 1979. Reproduction, spawning and development of the starfish *Patriella exigua* (Lamarck) (Asteroidea: Asterinidae) and some comparisons with *P. calcar* (Lamarck). *Aust. J. Mar. Freshwater Res.* **29**: 45–53.
- Marinovic, B. 1987. Reproductive biology of the protogynous hermaphroditic *Nototanaïs dimorphus* (Beddard), an antarctic tanaid. Masters Thesis, Univ. of California, Santa Cruz, CA.
- Menge, B. A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Lepasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.* **31**: 87–100.
- McEdward, L. 1984. Some relationships between egg size and the allometry of larval growth in echinoid plutei. *Am. Zool.* **24**: 46A.
- Oliver, J. S. 1979. Processes affecting the organization of marine soft bottom communities in Monterey Bay, California and McMurdo Sound, Antarctica. Doctoral Dissertation, Scripps Inst. of Oceanogr., La Jolla, CA.
- Pearse, J. S., and I. Bosch. 1986. Are the feeding larvae of the commonest Antarctic asteroid really demersal? *Bull. Mar. Sci.* **39**: 477–484.
- Perron, F. E. 1981. Larval biology of six species of the genus *Conus* (Gastropoda: Toxoglossa) in Hawaii, USA. *Mar. Biol.* **61**: 215–220.
- Rivkin, R. B., I. Bosch, J. S. Pearse, and E. J. Lessard. 1986. Bacterivory: a novel feeding mode in asteroid larvae. *Science* **233**: 1311–1314.
- Scheibling, R. E., and J. M. Lawrence. 1982. Differences in reproductive strategies of morphs of the genus *Echinaster* (Echinodermata: Asteroidea) from the eastern Gulf of Mexico. *Mar. Biol.* **70**: 51–62.
- Schoener, A. 1972. Fecundity and possible mode of development of some deep-sea ophiuroids. *Limnol. Oceanogr.* **17**: 193–199.
- Strathmann, R. R. 1971. The feeding behavior of planktotrophic echinoderm larvae: mechanisms, regulation and rates of suspension feeding. *J. Exp. Mar. Biol. Ecol.* **6**: 109–150.
- Strathmann, R. R. 1974. Introduction to function and adaptation in echinoderm larvae. *Thalassia Jugosl.* **10**: 321–339.
- Strathmann, R. R. 1979. Echinoid larvae from the northeast Pacific (with a key and comment on an unusual type of planktotrophic development). *Can. J. Zool.* **57**: 610–616.
- Strathmann R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Ann. Rev. Ecol. Syst.* **16**: 339–361.
- Strathmann R. R., and M. F. Strathmann. 1982. The relation between adult size and brooding in marine invertebrates. *Am. Nat.* **119**: 91–101.
- Vance, R. R. 1973. On reproductive strategies in marine benthic invertebrates. *Am. Nat.* **107**: 339–352.
- Young C. M. and F.-S. Chia. 1987. Abundance and distribution of pelagic larvae as influenced by predation, behavior, and hydrography. Pp. 385–442 in *Reproduction of Marine Invertebrates*, Vol IX, A. C. Giese, J. S. Pearse and V. B. Pearse, eds. Blackwell/Boxwood, Palo Alto, CA.